

Extent and Composition of Open Coastal Sandplain Plant Communities of the Cape
Cod National Seashore

by

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ABSTRACT

Coastal sandplain heathlands and grasslands of the northeastern United States are globally rare habitat types that support a unique assemblage of plants and animals. This habitat is rapidly disappearing due to plant succession following cessation of land use, and coastal processes. I used interpretation of historical maps, aerial photography, GIS, and analysis of field data to examine vegetation dynamics and the impact of historic land use and coastal processes on the current extent and composition of coastal sandplain plant communities found within the Cape Cod National Seashore (CCNS). Currently, one third (244 ha) of the coastal heathland and grassland habitat present at the inception of CCNS in 1961 still remains. Analysis and interpretation of time series aerial photography of sites (n=3) impacted by extreme land use shows that these areas follow a ~35-year successional path from bare mineral soil to predominately *Pinus rigida* shrubland or forest. Current extent and composition of coastal heathland is primarily determined by two factors: how recent and intense was historical land use at a site; and the influence of coastal processes, such as salt spray and sand deposition. Any influence by edaphic factors is likely confounded by past land use.

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PREFACE

This thesis is written in manuscript format specified by the University of Rhode Island Graduate School. The style follows the guidelines for submission as an original research article to the journal *Northeastern Naturalist*.

The coastal heathlands and grasslands of the Cape Cod National Seashore (CCNS) are globally rare landscape types which contain unique assemblages of plant and animal species. There is intense interest in preserving and restoring this habitat at a regional level. CCNS has identified the preservation and restoration of the biodiversity, aesthetics and cultural landscape of coastal heathlands as an important resource management goal.

This thesis examines the influence of past land-use and edaphic conditions on current extent and types of coastal heathlands and grassland in CCNS, and it examines the successional processes that have resulted in the gradual loss of these habitats. Results indicate that temporal proximity to, and magnitude of, land use disturbance are the main factors dictating extent and composition of coastal heathlands.

TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iii
PREFACE.....	iv
TABLE OF CONTENTS.....	v
LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
INTRODUCTION.....	1
Study area.....	2
Cultural landscape.....	3
Study habitats.....	4
Coastal sandplain grasslands.....	5
Coastal sandplain heathlands.....	6
METHODS	
Succession in Cape Cod National Seashore open coastal sandplain plant communities.....	9
Heathland land cover change, 1962-2001.....	9
Succession in open coastal sandplain plant communities, 1938-2001.....	10
Change in open coastal sandplain vegetation communities, 1988-1999.....	11
Data analysis.....	12
Current open coastal sandplain heathland and grassland habitat and relationships with environmental and land use categories.....	13
Data sources.....	13
Species characteristics.....	14
Environmental and land use data.....	14
Data analysis.....	15
RESULTS	
Plant succession in Cape Cod National Seashore open coastal sandplain heathlands and grasslands.....	18
Change in extent of Sandplain Heathland, 1960-2001.....	18
Plant succession in CCNS open coastal sandplain habitat, 1947-2001.....	18
Vegetation change in CCNS coastal sandplain habitat, 1988-1999.....	19
Current open coastal sandplain heathland and grassland plant communities and relationships to land use and environmental factors.....	20
Vegetation groups.....	20

DISCUSSION.....	23
CONCLUSION.....	28
TABLES.....	30
FIGURES.....	38
LITERATURE CITED.....	50
APPENDIX A.....	56
APPENDIX B.....	60
BIBLIOGRAPHY.....	61

LIST OF TABLES

Table 1a.	Area of coastal sandplain plant communities lost in the Cape Cod National Seashore, 1962-2001.....	30
Table 1b.	Area of coastal sandplain plant communities in the Cape Cod National Seashore, 1962-2001.....	30
Table 2.	Studies used in heathland vegetation community analysis.....	31
Table 3.	Results from ANOSIM analysis, power analysis of <i>P. rigida</i> cover values and descriptive statistics indicating increase or decrease of mean cover values (%) for selected species during sample period, 1988-1999.....	32
Table 4.	Mean area and patch size of CCNS coastal sandplain heathlands and grasslands.....	33
Table 5.	Vegetation groups identified by cluster analysis, along with species diversity indices, mean cover and frequency of plant species by group.....	34
Table 6.	Significant results from tests of physical features and land use categories between vegetation groups determined by cluster analysis.....	37

LIST OF FIGURES

Figure 1a.	Open area of Lower Cape Cod, 1949.....	38
Figure 1b.	Open area of Lower Cape Cod, 2000.....	38
Figure 2.	Location of CCNS coastal sandplain plant community sample sites.....	39
Figure 3.	Locations of three sites for studying successional processes in coastal sandplain plant communities at CCNS.....	40
Figure 4.	Diagram of permanent plots established by Carlson et al. (1992) and resurveyed in 1999.....	41
Figure 5a.	Aerial photographs of North Truro Sandpit site from 1960 (1:7200) and 1994 (1:5000).....	42
Figure 5b.	Aerial photographs of the Marconi Barrens Site #1 from 1960 (1:7200) and 1994 (1:5000).....	43
Figure 5c.	Aerial photographs of the Marconi Barrens Site #2 from 1947 (1:1500) and 1994 (1:5000) aerial photographs.....	44
Figure 6a.	Change in ground cover 1960-2001, Truro Sandpit Site	45
Figure 6b.	Change in ground cover 1960-2001, Marconi Barrens Site #1.....	45
Figure 6c.	Change in ground cover 1960-2001, Marconi Barrens Site #2.....	45
Figure 7.	Two-dimensional ordination of coastal sandplain heathland and grassland sample sites based on species cover data.....	46
Figure 8a.	Photograph of beach heather heathland group.....	47
Figure 8b.	Photograph of Sandplain Heathland (<i>A. uva-ursi</i> and <i>C. conradii</i> co-dominant) group.....	47
Figure 8c.	Photograph of Sandplain Heathland (<i>A. uva-ursi</i> dominant) group	48
Figure 8d.	Photograph of dune swale heathland group.....	48
Figure 8e.	Photograph of sandplain grassland group.....	49

INTRODUCTION

The coastal sandplain heathlands and grasslands of the northeastern United States and maritime Canada are globally rare ecosystems containing high biological diversity. The unique flora of coastal heathlands and grasslands has been recognized by botanists for over a century (Dunwiddie 1997), and these open coastal areas support the greatest concentration of rare or uncommon upland plant and animal species in the Northeast (LeBlond 1988; Carlson et al. 1992). The Massachusetts Natural Heritage and Endangered Species Program, The Nature Conservancy, and the U.S. National Park Service recognize the importance and rarity of the coastal sandplain grassland and heathland habitat (Massachusetts Rare Plants and Animals 2002; NPS 1998; Swain and Kearsley 2001; NatureServe 2004).

Open coastal heathlands and grasslands are restricted to glacial outwash and end moraine in coastal areas, and are typified by a diverse mosaic structure of micro-habitats (LeBlond 1988). The existence and extent of these open coastal landscapes are regulated by edaphic conditions (e.g., sandy, dry, nutrient-poor soils), frequent disturbance (e.g., coastal erosion, fire and agriculture), and plant succession and loss to development (Eberhardt 2001; Foster and Motzkin 2003; Dunwiddie 1998; Motzkin and Foster 2002; Motzkin et al. 2002).

Ironically, the same processes that have created and shaped these open coastal habitats are also the cause of the decline of this rare habitat. The coastal heathlands of Cape Cod National Seashore (CCNS) are being lost to succession and coastal

processes (Figs. 1a & 1b); from 1962 to 1985 there was a 63% loss of total area. The rate of loss was between 17 and 20 ha/yr from 1962 to 1985 (Carlson et al. 1992).

The loss of the coastal sandplain grassland and heathland habitat is of great interest to public and private management organizations in the northeast (Barbour et al. 1998; Breunig 2003). The CCNS General Management Plan recognizes that the coastal sandplain grasslands and heathlands are a globally, regionally and locally important natural and cultural resource, and instructs that:

“[Heathlands] will be preserved in various locations for their contribution to global biodiversity and to perpetuate the quality of open moors for cultural and aesthetic enjoyment”
(NPS 1998).

Study Area

Cape Cod National Seashore is a unit of the United States National Park Service encompassing over 16,000 hectares of the easternmost part of the Cape Cod peninsula in Massachusetts (Fig. 2). The study area is composed mainly of Wisconsin glacial outwash deposits, with the exception of the part of Truro north of High Head, and all of Provincetown (Fletcher 1993; Oldale and Barlow 1986). Provincetown and this section of Truro are composed of post glacial material scoured from the bluff face south of High Head and transported north and west by wave action and eolian processes (Allen et al. 1999; Fletcher 1993).

Cultural Landscape

Prior to European settlement, the easternmost part of the Cape was mostly forested, with heathland restricted to areas directly adjacent to the coast (<1 km) where wind, sand movement, and salt spray limited the growth of large shrubs and trees (Dunwiddie 1998; Dunwiddie and Caljouw 1990; Dunwiddie et al. 1996; Griffiths and Orians 2003; Motzkin and Foster 2002; Motzkin et al. 2002). There is little evidence of extensive heathlands or grasslands before the 1600s. Natural disturbance (e.g., blowdown and fires caused by lightning) and Native American land use practices, especially the use of fire to improve land for hunting and agriculture, may have increased the area of heathland, creating a dynamic mosaic of forest and heath. The use of fire to clear the understory of coastal forests allowed fire-adapted heathland and grassland species to expand into areas beyond those directly adjacent to the coast, allowing heathland communities to expand quickly when the forests were cleared by European settlers (Dunwiddie 1998; Parshall et al. 2003). Pre-European Native American land use (e.g., maize and gourd agriculture) has been suggested as the potential generator of extensive heathland habitat (Cronon 1983); however the archeological and paeleoecological evidence do not support this. Areas of high Native American population density do not correlate with high levels of charcoal or heathland pollen (Motzkin and Foster 2002; Parshall et al. 2003). Shifts in the climate of the North Atlantic region, resulting in rapid (decadal-scale) warming and cooling also may have influenced the frequency of fires, storm events, and distribution of plant communities leading to a possible increase in the area of coastal heathlands (Alley 2000; Alley et al. 1997).

The effect of European land use on the Lower Cape was dramatic. By the mid eighteenth century, at the height of agriculture on the Lower Cape, the land was ~60% open (Carlson et al. 1992; Dunwiddie et al. 1996; Parshall et al. 2003). The removal of trees, plowing, harrowing and grazing led to severe disturbance of the soil which strongly influenced future plant communities. By the turn of the century, poor soil, and a shift to a more industrial economy led to an abandonment of agricultural practices and subsequent establishment of shrublands and woodlands (Dunwiddie 1998; Eberhardt et al. 2003). The effects of a century of agriculture on the soil have resulted in a permanent change in the vegetation communities of the Outer Cape (Motzkin and Foster 2002).

The current landscape is a cultural artifact; current distributions of plant communities are not similar to pre-colonial distribution. The recognition that past land use exerts great influence, perhaps more than ecological processes, on current vegetation abundance and distribution must be considered in monitoring efforts of coastal sandplain communities (Eberhardt et al. 2003).

Study Habitats

The coastal sandplain plant communities considered in this study includes dune swales, grasslands and heathlands with generally <25% cover by shrubs and trees >1 m in height. Typical heathland species of the family Ericaceae and the genus *Hudsonia* have been present on the Lower Cape since ~12,000 years B.P. (Winkler 1985). The initial tundra-spruce parkland period from ~12,000 to 11,500 yr. B.P. indicates *Picea*, *Hudsonia*, and herbaceous species (e.g., composites) were present.

The abundance of heathland species in the pollen record declines dramatically by 11,000 yr. B.P. as the climate warmed and the tundra habitat changed to boreal forest (Winkler 1985). Evidence of heathland and grassland species continues in the pollen record at low levels (<1-4% of the total) until the arrival of European settlers 350 yr. B.P. (Motzkin and Foster 2002). After the arrival of European settlers, the amount of pollen from typical heathland and grassland species in pond sediment records increases, and is attributed to the land use practices of European settlers (Winkler 1985; Motzkin and Foster 2002).

Heathlands are the most abundant open habitat found at the CCNS. Only two large areas of grassland are found within the Park, both the result of recent agricultural activity and development. These are located at Fort Hill in Eastham, and at High Head/Pilgrim Heights in North Truro. Both of these sites contain a patchwork of areas dominated by sandplain grassland indicators (e.g., *Schizachyrium scoparium*), and by ericaceous shrubs (e.g., *Gaylussacia baccata*), pitch pine (*Pinus rigida*) and other non-typical species like velvet grass (*Holcus lanatus*), and woodbine (*Parthenocissus vitacea*).

Coastal Sandplain Grasslands

Coastal sandplain grassland is a globally endangered National Vegetation Classification System (NVCS) association, given a rank of G2 (imperiled) by The Nature Conservancy (Swain and Kearsley 2001), and with a distribution limited to the coastal areas of Massachusetts and to Long Island, New York (Dunwiddie 1998; Dunwiddie et al. 1996;). Coastal sandplain grasslands, considered an Eastern corollary to Midwestern prairies, is typically dominated by the bunch grass little

bluestem (*S. scoparium*), Pennsylvania sedge (*Carex pensylvanica*) and by other graminoids and forb species (Dunwiddie et al. 1996). These grasslands are located on exposed, dry, well-drained xeric soils that undergo frequent disturbance by wind, salt spray or human manipulation.

The typical structure of this habitat in the CCNS is a mosaic of very small patches, <1.0 ha at most, that blends into the surrounding sandplain heathlands and woodland habitats. In addition to the dominant grasses, this community usually contains some dwarf shrub species, especially the ubiquitous *Arctostaphylos uva-ursi*. Sandplain grasslands are not found at the CCNS to the extent found on Nantucket and Long Island where they can cover upward of tens of hectares (Dunwiddie 1998). Nearly all significant areas of sandplain grassland found on Cape Cod are the result of human activity: graveyards, power line rights-of-way, abandoned fields and roadways (LeBlond 1988). The small patchy quality of the heathland habitat at CCNS lessens its value as habitat for wildlife species that depend on grassland habitat, like the vesper sparrow (*Pooecetes gramineus*) (Kearney and Cook 2001). The management of this habitat is the key to its survival.

Coastal Sandplain Heathlands

Coastal sandplain heathland is a globally rare (NVCS) association, given the rank of G3 (vulnerable) by The Nature Conservancy (Swain and Kearsley 2001). They have a greater distribution than sandplain grasslands, found from the Pine Barrens of New Jersey to maritime Canada, but are most extensive on Nantucket and the easternmost part of Cape Cod (LeBlond 1988). Coastal heathlands are found

primarily on xeric sandy soils near the ocean, that are exposed to harsh wind, sand movement, and salt spray. Some areas of coastal heathland are found farther inland, but are restricted to areas of frequent human disturbance, primarily power line rights-of-way and areas of extreme soil manipulation (e.g., former military bases) (LeBlond 1988).

The sandplain heathlands of the CCNS are found primarily along coastal scarps on the east and west sides of the Lower Cape (Fig. 1b). *A. uva-ursi* is the dominant dwarf shrub of most of the CCNS heathlands, with *Hudsonia tomentosa*, or *Corema conradii* as co-dominants in parts of the Marconi Barrens area heathlands of Wellfleet and also in most Truro heathlands (Carlson et al. 1992). Extensive areas of pitch pine (*P. rigida*) woodland within the CCNS, especially in Wellfleet and Truro, have a dense understory of *A. uva-ursi* or *C. conradii* (Dunwiddie et al. 1993). The Marconi Barrens area of Wellfleet has the most extensive coastal heathlands; the largest continuous area identified by the CCNS 2000 vegetation map covers 14.3 ha (Sneddon and Zaremba 2004).

This study examines change in spatial extent of open coastal sandplain vegetation communities from 1960 to 2001 found in the CCNS, and successional process from bare sand at three test sites. It tests the hypothesis that (H_0) there has been no change in species abundance between 1988 and 1999. This study also examines the current extent and composition of coastal sandplain vegetation communities, with an emphasis on coastal sandplain heathlands. It tests the hypothesis (H_0) that there is no difference in the median values of historical land use,

and environmental and physical site features among heathland groups identified with cluster analysis.

METHODS

Succession in Cape Cod National Seashore open coastal sandplain plant communities

Heathland Cover Change, 1962-2001

Landscape-level data were collected previously for the years 1962, 1979, 1985 (from Carlson et al. 1992), and by my study for 2001. Methods from the Carlson et al. (1992) study and this study follow respectively.

Areas of heathland vegetation (*A. uva-ursi*, *Hudsonia* spp., *C. conradii*) were identified using CCNS vegetation maps from 1962 and 1979 prepared by the NPS Denver Service Center. Major heathland areas were defined (contiguous patches of heathland vegetation $\geq 400 \text{ m}^2$) in 1988 by site visits and stereoscopic analysis of CCNS color-infrared orthophotographs from 1985 (1:25000) and 1987 (1:7200). Smaller patches were not identified due to limitations resulting from the scale of working images and maps (Carlson et al. 1992). Polygons of heathland areas $\geq 400 \text{ m}^2$ were delineated on Mylar overlays on the color-infrared orthophotographs (1:25000). The polygons were then digitized using ARCINFO; areas of heathland polygons were then calculated.

In 2003, existing GIS polygons of heathland areas identified in 1988 were projected on the half-meter resolution, 1:5000-scale true-color orthophotographic imagery, collected in April of 2001 (MA GIS 2004a). The boundaries of the 1988 polygons (from Carlson et al. 1992) were used as a guide for calculation of current heathland area. Current technology allows for analysis at a finer resolution than

available in 1988; however, by restricting analysis to the areas identified in 1988, the analysis is of the same data and is kept at a similar scale and resolution. New polygons (shapefiles) representing heathland, using the 1988 polygons as guides, were created in ARCMAP 8.3 (ESRI Redlands, CA). Site visits were conducted to confirm polygon delineations; UTM coordinates were collected at edges of heathland habitat with a Garmin GPSmap 76S, a 12-channel, real-time, differentially corrected (WAAS) GPS unit allowing <3-m accuracy. The areas of these polygons were calculated (with ARCMAP 8.3), and rates of change (in ha) were calculated using the areas of heathland habitat identified by the 1962 and 1978 vegetation maps, the 1988 analysis (Carlson et al. 1992), and by analysis in 2003.

Succession in CCNS Open Coastal Sandplain Plant Communities, 1938-2001

Three sites within the CCNS were selected to study succession in coastal heathlands at a finer scale (Fig. 3) -- two areas in a former Army bombing range in the Marconi Barrens Area (Wellfleet, MA), and an abandoned sand pit in North Truro Massachusetts -- for similar site history, and intensity of impact to the vegetation community. Each site was similarly impacted; vegetation, including lichens and mosses, and organic soil horizons were removed exposing bare sand. A series of aerial photographs was collected from the CCNS photograph archive, and from Massachusetts GIS (MAGIS 2004b) for each site. These included pre-impact photographs for the North Truro site (1947; 1:1500) and the Wellfleet sites (1938), and of the study series 1960 (1:7200), 1977, 1987, 1994 (1:5000) and 2001.

Photographs that were not already in a digital format (1938-1987) were digitized and georeferenced using ARCMAP 8.3.

Three habitat types were identified for each site in each year: 1) bare sand; 2) ground cover and plants <1 m, including lichens, mosses herbs and short shrubs; and 3) tall shrubs and trees >1 m. These strata were chosen because it allows NVCS habitat definitions to be applied; an area covered by >25% of >1 m shrubby vegetation is no longer considered open heathland habitat (Grossman et al. 1998). Each habitat type was mapped and converted to a GIS shapefile for each year. The minimum mapping unit was $\sim 5 \text{ m}^2$ with boundaries determined by the tone and sharpness of shadow. Habitat type polygon had to contain $\sim 75\%$ of the requisite cover to be classified. When available (for all but the 2001 series), the aerial orthophotographs were examined with a stereoscope to confirm polygon classification. Site visits were conducted in 2003 to confirm polygon classification for the 2001 series. The area (ha) of each polygon was calculated (ARCMAP 8.3).

Change in Composition of CCNS Open Coastal Sandplain Vegetation Communities 1988-1999

In 1988, Carlson et al. (1992) used the 1979 CCNS vegetation map to identify heathland areas $\geq 400 \text{ m}^2$. Twelve heathland sampling sites were established, each with two replicate vegetation survey plots. Replicate sampling plots were subjectively located in each selected heathland area to ensure adequate representation. The long axis of each sample plot was 10 m x 20 m and aligned (magnetic) north to south. Each plot was marked in the southwest corner with a cement filled PVC pipe, and at the

corners with capped rebar driven into the soil. The beginning and end of three transects at 1 m, 11 m and 19 m consisting of 10 1-m x 0.25-m contiguous quadrats also were marked with capped rebar (Fig. 4). In each quadrat, ground and canopy vascular plants, lichens and mosses were identified to species when possible, and the cover of each assigned to a cover class (1 = <1%; 2 = 1-5%; 3 = 6-25%; 4 = 26-50%; 5 = 51-75%; 6 = 76-100%).

In 1999, the plots at all the sites were revisited. Site maps and field notes from 1988 were used to locate the sites. A compass, transect tapes and a magnetometer were used to locate all rebar corner and transect stakes. All of the sample sites, plots and subplots were located. Vascular plants, lichens and mosses were identified to genus, and most to species; ground and canopy cover were estimated in each sub-plot (1 m x 0.25 m) using the same cover class ranks as used in 1988. For analysis, the mean abundance was calculated for each species for each site using the mid-point of the observed cover class (e.g., Motzkin et al. 2002; Peet et al. 1998)

Data Analysis

To determine the impact of plant succession, the similarity in species composition and relative abundance between years (1988 vs. 1999) at each site was tested. A non-parametric multivariate analysis of similarities (ANOSIM: Clarke and Greene 1988) was conducted on a similarity matrix of Bray-Curtis distances (Bray and Curtis 1957) calculated from the subplot species abundance values. A Bonferroni correction ($\alpha=0.05$) was applied to adjust the experimental error for the number of pair-wise comparisons for each analysis (Zar 1999). This test was selected because it

has minimal assumptions (e.g., no specific distribution, or balanced numbers of replicates).

The species that contributed most to the observed dissimilarity between years at each site were identified with SIMPER (Clarke and Ainsworth 1993). Analyses were conducted with the PRIMER 5 (PRIMER-E 2003) software package.

A power analysis was conducted on *P. rigida* mean abundance values by sample site. Pitch pine was selected because it is recognized as the species most frequently encroaching open coastal heathland habitat (Dunwiddie et al. 1993). The power analysis compared the means of two *P. rigida* sample populations with unequal variances. It was two tailed and assumed the normal distribution with $\alpha=0.1$. All tests were conducted using the online power calculator provided by the Statistics Department at the University of Southern California (USC 2004).

Current open coastal sandplain heathland and grassland habitat and relationships with environmental and land use categories.

Data Sources

Recent ecological studies at CCNS with vegetation cover data and site environmental data of coastal heathland habitat were reviewed. Data sets from studies at different heathland habitat sites were selected that were temporally as close as possible (Table 2) and that followed methods comparable to those suggested by the NVCS for vegetation cover: 20-m x 20-m plot area with generally <25% canopy (Grossman et al. 1998). Twenty eight sites were selected to classify sandplain heathland and grassland types (Fig. 2).

The confounding impact of analysis of data collected with similar, yet different methods in different years is recognized; however, the impact is considered minimal in light of the results. The ordination of the cover data generally groups sites in a meaningful way, and the increase in sample size, larger spatial distribution and exploratory nature of this study justify the methods. In all the studies, plant cover data were collected during the summer and early fall, the height of growing season and peak standing biomass for most species encountered. In all cases, the cover data were estimated using cover classes; the mid-point of the cover class was used for analysis.

Species Characteristics

Plants were identified to genus, most to species, following Gleason and Cronquist (1991). Updated taxonomy and information on species characteristics (e.g., non-native, invasive or rare) were gathered from the USDA PLANTS database (USDA NRCS 2004). Additionally, a subset of species characteristic data from the USDA PLANTS database was collected for further analysis (e.g., tolerance to environmental conditions, bloom period, active growth period).

Environmental and Land Use Data

Environmental data were collected in 2003 from the field for this study using the following methods: three 30-cm deep soil samples were collected from each plot with a 5- x 15-cm steel sleeve hammer corer. Soil samples were allowed to air dry. All soil samples from each plot were homogenized and analyzed by the North Atlantic Coastal Lab (NPS-North Truro, MA) for total C and N (CNS Flash 21111 Thermo-Finnegan), and at Brookside Labs (New Knoxville, OH) for texture, pH (H₂O 1:1),

extractable nutrients (Mehlich 1984) and percentage organic matter (Storer 1984). Procedures and analysis included: percent total nitrogen, percent total carbon, C:N ratio, percent clay+silt, total exchange capacity (TEC; millimole/100 g soil), pH, percent organic matter and phosphorous (as P_2O_5) calcium, magnesium and potassium (mg/kg).

Data Analysis

Twenty-eight sample sites were spatially categorized by geologic feature using GIS data layers (soil type, surface geology and geographic unit) generated from the Barnstable County Soil Survey (Fletcher 1993). Sites also were assigned an impact index based on historical and recent land use interpreted from 1848 coastal survey maps, from 1949 land use maps and 2001 aerial photographs (MAGIS 2004b).

Untransformed species abundance (cover) scores were used to ordinate and classify vegetation groups. All ordination and classification used the Bray-Curtis distance to quantify dissimilarity among the sample sites (Bray and Curtis 1957). Sites were clustered (using PC-ORD 4 software, McCune and Mefford. 1999) based on species abundance using the Grieg-Smith flexible β linkage ($\beta = -0.25$) method (Grieg-Smith 1983).

Indicator species and common (most abundant) species were identified for each group. Two routines were performed on each group identified by cluster analysis: indicator species analysis to identify species with strong affinity to each group (Dufrene and Legendre 1997), and similarity percentage (SIMPER) procedure to identify the abundance and similarity of groups (Clarke and Ainsworth 1993).

These procedures were performed with PC-ORD 4 and PRIMER 5 software packages, respectively.

A multidimensional scaling (MDS) ordination technique was used to create a two-dimensional scatter plot diagram of the sample plots in ordinal space (conducted with the PRIMER 5 software package). One hundred iterations of the algorithm were computed from a random starting point (Kruskal 1964). The final stress of the two dimensional ordination of all sample plots was moderate (*Kruskal's stress formula* $I=0.14$); a three dimensional ordination did not significantly reduce the stress (*Kruskal's stress formula* $I=0.10$) (Kruskal 1964). Considering the inherent high dimensionality of the data set, i.e. 28 sample sites and 107 “species,” this level of stress can be considered low enough to acceptably represent the structure of the data (Kruskal and Wish 1978; Clarke and Ainsworth 1993). Comparing the results of the cluster analysis with the MDS plot confirms that the ordination is effective, i.e. groups identified in cluster analysis are readily evident in MDS plot (Clarke and Warwick 2001; McCune and Grace 2002).

Difference between groups determined by cluster analysis and environmental categories (e.g., land use, geology) was tested using the G tests of independence (Zar 1999). Kruskal-Wallis tests were conducted to test if edaphic features and species characteristics (e.g., shade tolerance, salt tolerance) of groups identified with cluster analysis varied significantly from expected population medians. In both cases, *post hoc* tests were conducted to identify differences between cluster groups. The *post hoc* tests were experimentwise-corrected to $\alpha=0.05$ using the Bonferroni method (Zar

1999). All G-tests of independence and Kruskal-Wallis tests were conducted with XL STAT software (XL STAT 2002).

RESULTS

Plant succession in Cape Cod National Seashore open coastal sandplain heathlands and grasslands

Change in Extent of Sandplain Heathland, 1960-2001

The Cape Cod National Seashore has been losing ~12 ha of coastal heathland per year since 1962 (Table 1a) (Carlson et al. 1992). Approximately one third of coastal heathland present when the Seashore was established now remains (Table 1b). The rate of loss slowed from ~17 ha/yr in the sample periods of 1962-1979 and ~20 ha/yr 1979-1985 to ~5 ha/yr from 1985-2001 (Table 1a), a four-fold reduction in the rate of loss indicating slowing of the succession process.

Plant Succession in Open Coastal Sandplain Habitats, 1947-2001

Analysis of aerial photography (Fig. 5a-c) indicated that within the first ~10 years of termination of disturbance (Early 1940s for Marconi Barrens Site #1 and 1960 for the other two sites), the three study sites were rapidly covered by vegetation (including lichens and mosses) of <1 m (Fig 6a-c). The character of the habitat changed from bare, open and sandy, to predominately ($\geq 50\%$ cover) covered by lichens, grasses and low shrubs; habitat typical of coastal heathlands (Grossman et al. 1998).

Within the first ~35 years of termination of disturbance, the three study sites were covered >25% by vegetation >1 m (Fig. 6a-c); this shrub and tree overstory altered the habitat, and although typical heathland species may continue in the understory at these sites, the site would be considered shrub barrens, not heathland (Grossman et al. 1998). The Truro Sandpit site has experienced less increase in the

cover of >1m vegetation in the ~35 years due possibly to the continued use of the area as a dirt bike track.

Change in Composition of CCNS Open Coastal Sandplain Plant Communities, 1988-1999

The result of ANOSIM analysis between years at each site indicates that there has been little change in the vegetation during the sample period (Table 3). Only three sites had Global *R* values near or greater than 0.3, indicative of a weak increase in dissimilarity of vegetation cover values between years (Clarke and Greene 1988).

The results of the power analysis (Table 3) indicate that the pilot study was likely to detect change in *P. rigida* cover values only where there was a large change in cover. Thus the pilot study was unlikely to be successful in detecting change at sites that underwent little or no change in cover values, or where the within site variance was high.

Differences in cover values for important heathland, tree and shrub species were calculated (Table 3). Eight of the 12 sites saw an increase in the cover of *A. uva-ursi*; four of those saw an increase in cover of >20%. Typical heathland species (e.g., *C. conradii*), and to a lesser extent, typical encroaching shrubs (e.g., *P. rigida* and *Q. ilicifolia*) both generally increased in cover.

Current open coastal sandplain heathland and grassland plant communities and relationships to land use and environmental factors

The coastal sandplain heathlands and grasslands were mapped as part of the 2000 CCNS vegetation map (Sneddon and Zaremba 2004) (Fig. 1b). I calculated spatial descriptive statistics (mean area, patch size) with ArcMap software (Table 4) (ESRI 2004).

Five vegetation groups were identified by cluster analysis (Table 5) and plotted in ordinal space (Fig. 7). The abundance and frequency of *A. uva-ursi*, *C. conradii* and *H. tomentosa* define the three main heathland groups, and the grass *S. scoparium* characterizes the sandplain grassland group. The final group, dune swale heath, describes plant communities found in swales among the dune system in Provincetown, MA.

Vegetation Groups (Fig. 8a-e respectively)

1) Beach heather heathland: This group is composed mostly of diverse, open, bluff-edge sites (median distance to ocean/bay 219 m). The co-dominant species include stunted *P. rigida* shrubs and *A. uva-ursi*, with *H. tomentosa* and *Ammophila breviligulata* becoming abundant closer to the bluff edge as sand deposition increases. Many shrubs (e.g., *Prunus maritima* and *Morella pennsylvanica*), herbs (e.g., *Lechia* spp. and *Polygonella articulata*.) and graminoids (e.g., *Deschampsia flexuosa* and *C. pennsylvanica*) typical of depauperate areas are frequently found, although not at high abundance (Table 5).

2) Sandplain heathland (*A. uva-ursi* and *C. conradii* co-dominant): These sites are mostly inland (median distance to ocean/bay 802.5 m), sheltered sites typified by a thick carpet of *A. uva-ursi* and *C. conradii* with a sparse overstory of *P. rigida* and to a lesser degree, other shrubs (e.g., *Q. ilicifolia*, *G. baccata* and *Vaccinium* spp.). There are infrequent sandy openings where lichens, herbs and graminoids are found.

3) Sandplain heathland (*A. uva-ursi* dominant): These sites are typified by a thick carpet of *A. uva-ursi*, with *P. rigida* and *Q. ilicifolia* shrubs forming a sparse canopy layer. *C. conradii* is found in low abundance at a few sites. This is the most abundant type of coastal sandplain heathland found at CCNS.

4) Dune swale heathland: This group describes the plant community in many of the dune slacks in the dune systems of Provincetown, MA. The soil is typically sandy and depauperate (Appendix A, Table 8). The vegetation consists of a sparse *P. rigida* overstory, shrubs (e.g., *M. pensylvanica* and *Vaccinium angustifolium*), herbaceous vegetation (e.g., *P. articulate*) and graminoids, especially *D. flexuosa*.

5) Sandplain grassland: These two sites represent areas that were used for cultivation, pasture or located in the parade grounds of a former U. S. Army base, then subsequently abandoned when the CCNS was established. The group is differentiated from other sites with a similar land use history by the abundance of the grass *S. scoparium*.

G tests of independence were used to determine if vegetation groups identified by cluster analysis occurred disproportionately due to past land use or geologic features (Table 6). The null hypothesis (no difference between groups identified by cluster analysis) was rejected in the surface geology, land use (1848 and 1949) and impact index categories, indicating that the dune swale sites are different from all the other groups. This reflects the fact that these sample sites have been dunes since at least 1848, and that they continue to be dunes. This indicates the influence and continuing impact of geology and geography on vegetation communities (Table 6). Results from other test can be found in Appendix A.

Kruskal-Wallis tests were conducted to determine if vegetation groups identified by cluster analysis differed in edaphic or species characteristics. The null hypothesis was rejected only to separate sandplain grassland from the others groups based on the lower ratio of plants adapted to coarse sediment.

The small sample size ($n=28$) and the variable nature of the data make detecting anything but large differences very difficult, and make interpretation challenging.

DISCUSSION

The current vegetation of the Cape Cod National Seashore is in all likelihood very different from that found by the Europeans during the 16th and 17th centuries (Motzkin and Foster 2002). The landscape of easternmost Cape Cod before western contact is difficult to describe, especially the heathland component. Pollen records from Cape Cod and Martha's Vineyard pond sediments indicate that members of Ericaceae and Graminae (families containing common heathland species) were present since the last glaciation (Parshall et al. 2003; Winkler 1985). Historical documents vaguely describe the land use practices of Native Americans, e.g., use of fire and agriculture, and the extent of open areas resulting from Native American land use practices (Cronon 1983; Foster and Motzkin 2003; Kneeder-Schad et al. 1995; Motzkin and Foster 2002; Patterson and Sassaman 1988). Whatever the impact of Native American land use practices on the Lower Cape landscape was, heathland species (*A. uva-ursi*, *C. conradii*, *G. baccata*, *Hudsonia* spp.) were present, and expanded greatly in the wake of European settlement and subsequent removal of most of the Lower Cape forests (Eberhardt et al. 2003; Motzkin and Foster 2003).

The clearing of most of the Lower Cape by the 1800s allowed for the distribution of heathland species across the landscape. After the discontinuation of extensive agriculture on the Lower Cape by the end of the 19th century (Altpeter 1937; Motzkin and Foster 2002), open areas populated by typical heathland species slowly transformed into the current pine/pine-oak forests following a succession pattern of increasing structural complexity: lichen (*Cladonia* spp.) and algal soil crust; beachgrass (*A. breviligulata*) in areas of active sand movement; beach heather (*H.*

tomentosa); bearberry (*A. uva-ursi*), and broom crowberry (*C. conradii*); black huckleberry (*G. baccata*) and lowbush blueberry (*Vaccinium angustifolium*); Pitch Pine (*P. rigida*) and oak (*Quercus* spp.) shrubland; pitch pine (*P. rigida*) and oak (*Quercus* spp.) woodland.

Heathland and grassland species continue to be found in the understory of many shrubland and woodland types, and in small open patches scattered throughout the pine/pine-oak forest (Chokkalingam 1995; Eberhardt et al. 2003). Although heathland species are found throughout the entire CCNS, open habitat (<25% shrub and tree cover) with the requisite heathland species is limited, for the most part, to areas that have been severely impacted within the last 50 years (Figure 1a-b).

Data from my study (Figure 6a-c) indicate that under the most severe circumstances (i.e., removal of all vegetation and exposure of mineral soil); abandoned open areas will become shrubland/forest in approximately 30 years. If this represents a conservative estimate, then areas that were not as severely impacted would revert to shrubland/forest in less time. This supposition is generally supported by CCNS forest stand age; secondary shrubland and forest types were approximately 40 to 80 years old; plowed areas (i.e., higher disturbance) younger and former woodlots older (from Eberhardt et al. 2003).

Since the establishment of the CCNS in 1961, secondary succession has generally proceeded unhindered throughout the Park. In the first 20 years, a third of the heathland changed from plants <1 m tall to plants >1 m; mostly shrublands and forest (Table 1b). However, the rate of loss slowed from almost 20 ha/yr during the periods between 1962 and 1985 to approximately 5 ha/yr between 1985 and 2001.

Certainly, some of this four-fold reduction in the rate of loss is due to differences in analytical methods and interpretation of orthophotography and GIS coverages; however, such a large reduction indicates some slowing in the rate of loss (Table 1a).

This reduction in rate of loss is borne out by the analysis of change in heathland vegetation. From 1988 to 1999, there was little change in plant species abundance values in 12 heathland monitoring sites (Table 3). In fact, many of the plots showed a gain in cover of *A. uva-ursi*, a species that is relatively shade intolerant, generally indicating that there has been little expansion of an overstory (Table 3). Three sites (01, 05, 08) showed a weak increase in dissimilarity. Two of these sites (05 and 08) are sandy and depauperate; one is very close to a coastal bluff (08) the other is in a high impact area (05, a former sandpit). At both of these sites, there was an increase in *A. uva-ursi* abundance, an indication that these sites are possibly in the process of changing community character. Site 05, is revegetating after removal of all vegetation and exposure of mineral earth in the late 1950s (see figure 5a for an aerial photo of this site). Site 08, located on an exposed bluff overlooking Cape Cod Bay, may be changing from a *H. tomentosa* (note 15% loss in cover of this species) dominated system, to an *A. uva-ursi* dominated system, possibly due to *H. tomentosa* stabilizing the sandy soil and making the site suitable for expansion of *A. uva-ursi*. Site 01, a site close to the bluff edge in the Marconi Barrens area (former Camp Wellfleet), and site 08, located on an exposed bayside bluff, is slowly being invaded by *P. rigida* shrubs. Site 01 is located on a former road bed in a small hollow protected by two dunes. Most of the surrounding area has already reverted to scrub

pine barrens; the impact to the site by a military base road (removed in the early 1960s) was perhaps enough to slow encroachment by the surrounding pines.

Power analysis of *P. rigida* cover values indicates that some caution is warranted with interpretation of the data (Table 3). In the case of *P. rigida*, the pilot study was effective at successfully detecting change in sites where the change in abundance was great, such as at site 01 where there was a mean increase of 13.8%. At sites with smaller changes in abundance, or where the variance was great, the pilot study was generally not effective at detecting change.

The slowing in the heathland loss rate can be interpreted as slowing of the successional process. Most of the CCNS heathlands are reaching a point where the next step in succession is retarded, due to a combination of current management practices (e.g., mowing powerline rights-of-way), coastal processes (e.g., salt spray) and impact of intense historical land-use practices (e.g., military base). In some cases, especially in the Marconi Barrens area, succession has essentially stopped; certain sites will continue on as heathland or other open habitat and likely never become pine woodland (LeBlond 1988).

Although recent studies of the CCNS upland forests indicate that the influence of past land use, i.e. if a site was plowed or a used as a woodlot, has a detectable result on the composition of current vegetation communities (Chokkalingam 1995; Eberhardt et al. 2003; Motzkin and Foster 2003; Parshall et al. 2003), the results of my study indicate that most, if not all current heathland habitat at CCNS is the product of direct spatial proximity to oceanic influence and temporal proximity to, and magnitude

of, land use disturbance (Table 6) (Dunwiddie et al. 1996; Foster and Motzkin 2003; Motzkin and Foster 2002).

Most current sandplain heathland at CCNS is located in the areas that were recently (within the last ~40 years) impacted by intense disturbance, and may be experiencing continuing ecological stress, i.e. sand deposition, salt spray and loss of habitat to coastal erosion (Dunwiddie et al. 1996). Salt spray has been implicated as one of the major stressors on the coastal communities, limiting the encroachment of shrubs and trees, and defining the extent of open coastal areas (Boyce 1954; Griffiths and Orians 2003). Sand deposition (i.e., burying of plants), and impact of wind (e.g., physical damage by buffeting) may also be responsible for community distribution not only directly adjacent to the coastal bluffs, but at some inland sites (LeBlond 1988)

Five coastal heathland vegetation communities were identified by ordination of cover data (Table 5 and Fig. 7). Similar groups were identified by other studies (Carlson et al. 1992; Dunwiddie et al. 1993). There were no significant differences between groups distinguished by cluster analysis based on edaphic factors (Appendix A). Any edaphic factors that may have influenced heathland distribution are likely confounded by historic land use.

CONCLUSIONS

Current coastal heathland areas represent the last vestiges of the open landscape that dominated the easternmost part of Cape Cod during the last century and a half. Land use, mainly agriculture, was the driving force in the creation and maintenance of these open habitats. As agriculture declined, shrub barrens, woodland and forest became the most common vegetation types with heathland habitat persisting only in areas that were impacted by modern land use practices or continuing coastal processes.

The results of this study indicate a slowing but continuing loss of coastal heathland habitat. The plants and animals that use coastal heathland habitat, including some species endemic to heathland habitat, will continue to decline with this dwindling habitat. Most large contiguous areas of sandplain heathland are gone (Table 4); the average patch size is approximately 1.9 ha, a size considered insufficient for supporting uncommon species such as vesper and grasshopper sparrows (*Ammodramus savannarum*) (Kearny and Cook 2001). This fragmented habitat also may limit propagation of plant species such as *C. conradii*, a shrub common to CCNS heathland (MA species of special concern), whose seeds are dispersed by ants (Dunwiddie 1990).

Nearly all the CCNS heathlands are the direct result of historical land use. There is no evidence of extensive open habitat before European contact. Any heathland habitat extant prior to European impact was likely found in disjointed, isolated and spatially plastic micro-habitats along the coastal bluff, the constantly changing result of erosion, salt spray and eolian processes. Current species

assemblages may have only come into being when the coastal forest was removed providing an ample and new area to populate.

This does not diminish the importance of current CCNS sandplain heathland and grassland habitat; however, it must be understood that these habitats are not naturally sustaining and, without human intervention, will eventually disappear (Foster and Motzkin 2003). These open areas are valued as a link to the culture and agrarian past of the CCNS, and for their significant biological diversity (NPS 1998). The future of coastal heathland habitat depends on effective and continuing monitoring and direct management action, including a variety of methods: cutting, fire, returning areas to pasture, and perhaps application of herbicides.

Table 1a. Area (ha) of coastal heathland lost by town 1962 to 2001. Bold indicates gain in coastal heathland area. The last column indicates the rate of loss of coastal heathland (ha/yr) for each sample period.

Years	Eastham	Wellfleet	Truro	Provincetown	CCNS Total	Loss Rate (ha/yr)
<i>62-79</i>	<0.1	267.5	56.1	n.d.	285.9	16.8
<i>79-85</i>	0.7	44.9	49.9	23.0	117.0	19.5
<i>85-01</i>	3.7	39.2	34.6	4.1	81.6	5.1
<i>62-01</i>	-	-	-	-	-	12.4

Table 1b. Area (ha) of coastal heathland by town 1962 to 2001. Data from 1962 and 1979 are from Carlson et al. (1992).

Year	Eastham	Wellfleet	Truro	Provincetown	CCNS Total	% 1962 total
<i>1962</i>	7.0	462.0	260.0	n.d.	728.9	100.0
<i>1979</i>	7.0	194.5	203.9	37.7	443.0	60.8
<i>1985</i>	7.7	149.6	154.0	14.7	271.1	37.2
<i>2001</i>	4.1	110.4	119.3	10.6	244.5	33.5

Table 2. Information about studies used to compile data set used for cluster analysis.

<i>Study</i>	<i>year data collected</i>	<i># sites</i>
Barrett and Gwilliam (1999)	1999	2
Cook and Boland (2001)	2000	2
Gwilliam (2004)	2003	18
Smith and Potash (2004)	2001	6

Table 3. Results from ANOSIM analysis, power analysis of *P. rigida* cover values, and descriptive statistics indicating increase or decrease of mean cover values (%) for selected species during sample period, 1988 to 1999.

Site ID	01*	2	3	4	05*	6	7	08*	9	10	11	12
Global <i>R</i>	0.342	0.232	0.149	0.237	0.294	0.25	0.182	0.336	0.111	0.115	0.194	0.257
Power	0.91	0.45	0.10	0.22	0.50	n.a.	0.57	0.84	0.42	n.a.	0.36	0.74
<i>Arctostaphylos uva-ursi</i>	-6.3	10.2	5.2	27.3	20.2	-3.7	1.4	40.3	-4.8	22.2		18.3
<i>Corema conradii</i>	0.6	9.5	17.7		6.6	3.4	2.9		2.3			5.6
<i>Hudsonia ericoides</i>	1.3	2.0	-1.4		-5.6			-0.6				-0.5
<i>Hudsonia tomentosa</i>	-5.9	-3.1		-0.7	4.4			-15.0		0.4		
<i>Deschampsia flexuosa</i>	0.3	-0.9		2.9	3.3	-15.0	-4.4	1.3	5.3	2.5	2.1	0.5
<i>Schizachyrium scoparium</i>	0.3	0.6		0.3	< 0.1		0.3	0.6	0.4			
<i>Pinus rigida</i>	13.9	9.4	0.5	3.9	5.8		10.1	12.3	2.2		4.1	-11.6
<i>Quercus ilicifolia</i>	< 0.1	0.5	-1.6			6.8		0.3	< 0.1			-12.8
<i>Vaccinium angustifolium</i>				0.03	0.1		0.1		< 0.1			
<i>Vaccinium pallidum</i>			-0.3		-0.1	-0.1	-0.08					
<i>Prunus maritima</i>				0.1		-3.9			0.5	0.3		
<i>Prunus serotina</i>						-0.3		0.5				
<i>Morella pensylvanica</i>	-0.8	1.0		-11.8		-1.6	-1.6		-0.3	0.9	2.3	-1.4
<i>Gaylussacia baccata</i>			2.8						1.1			2.3

Global R: *R* statistic is ~0, similarity of vegetation composition abundance between and within years is the same on average (i.e. null hypothesis true). *R* statistic ~1, no similarity exists between years. One thousand permutations were calculated for each test resulting in $p < 0.001$ for all plots. (*) indicates sites with strongest dissimilarities between years.

Power (1- β): Value indicates the probability of pilot study design to correctly reject a false null hypothesis, i.e., successfully detect change in the cover values of *P. rigida* from 1988 to 1999. This analysis assumed a normal two-tailed distribution of two populations with unequal variance, $\alpha=0.1$ (USC 2004).

Table 4 Mean area and patch size (ha) of CCNS coastal sandplain plant communities. Information for this analysis was extracted from the 2000 CCNS vegetation map (Sneddon and Zaremba 2004).

<i>Habitat Type</i>	<i>Area (ha)</i>	<i>Mean Patch Size (ha)</i>	<i>SD</i>
<i>Coastal Sandplain Heathland</i>	202	1.3	2.1
<i>Coastal Sandplain Grassland</i>	5	0.9	0.7
<i>Beach Heather Heathland</i>	93	3.6	11.4

Table 5. Vegetation groups identified by cluster analysis, including species diversity indices, mean cover and frequency of plant species by group as identified by cluster analysis. (Only species found in more than three sites are listed.)

Average cluster similarity indicates the percent similarity of all the sample sites that were within each cluster group, as determined by SIMPER analysis. \bar{X} = mean cover value for species in cluster. fr =percent of sites comprising cluster that species is encountered.

Bold species "typify" group; these species are the most common to the clustered group and have been determined to contribute ~75% of intra-cluster similarity as determined with SIMPER analysis (Clarke and Ainsworth 1993).

Grey highlight indicates species identified as significantly ($p < 0.05$) representative of cluster as determined by Indicator Species Analysis (Dufrene and Legendre 1997).

Table 5.

	Beach Heather Dune Shrubland		Sandplain Heathland (<i>A. uva-ursi</i> and <i>C. conradii</i> co-dominant)		Sandplain Heathland (<i>A. uva-ursi</i> dominant)		Dune Swale Heath		Sandplain Grassland	
	(n=5)		(n=8)		(n=11)		(n=2)		(n=2)	
Avg. Cluster Similarity (%)	31.04		62.99		60.98		25.87		28.82	
Total Species (S)	16		13		15		9		36	
Species richness (Margalef)	3.66		2.56		2.97		2.37		9.13	
Pielou's Evenness	0.55		0.56		0.41		0.43		0.51	
Shannon's Diversity Index (log e)	1.52		1.41		1.03		0.93		1.83	
	fr.	X	fr.	X	fr.	X	fr.	X	fr.	X
<i>Pinus rigida</i> P. Mill.	100%	14.4	100%	18.5	91%	15.5	100%	5.9	100%	3.8
<i>Deschampsia flexuosa</i> (L.) Trin.	80%	0.4	75%	0.6	91%	0.9	100%	6.1	100%	5.8
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	100%	13.3	100%	31.6	91%	63.1			100%	3.44
<i>Carex pensylvanica</i> Lam.	100%	1.6	63%	0.4	64%	0.9			100%	1.1
<i>Schizachyrium scoparium</i> (Michx.) Nsh	80%	0.1	38%	<0.1	100%	0.7			100%	33.9
<i>Quercus ilicifolia</i> Wangenh.	100%	1.4	50%	4.8	91%	6.2			50%	0.2
<i>Morella pensylvanica</i> (Mirbel) Kartesz, comb. nov. ined.	60%	1.9	38%	0.3	64%	1.3	50%	0.3	50%	0.4
<i>Ionactis linariifolius</i> (L.) Greene	40%	<0.1	50%	<0.1	64%	<0.1			100%	<0.1
<i>Lechea maritima</i> Leggett ex B.S.P.	60%	<0.1	38%	<0.1	55%	<0.1			100%	0.3
<i>Vaccinium angustifolium</i> Ait.	20%	1.9	75%	0.8	45%	1.2	50%	0.1	50%	0.2
<i>Ammophila breviligulata</i> Fern.	60%	0.2	38%	<0.1	27%	1.5	50%	0.1	50%	<0.1
<i>Pityopsis falcata</i> (Pursh) Nutt.	60%	<0.1	25%	<0.1	36%	<0.1	50%	0.1	50%	<0.1
<i>Hudsonia ericoides</i> L.	20%	0.9	63%	2.9	36%	0.3	50%	0.1	50%	0.9
<i>Corema conradii</i> (Torr.) Torr. ex Loud.	40%	0.9	100%	31.5	55%	8.5				
<i>Solidago sempervirens</i> L.	60%	<0.1	13%	0.1	9%		50%	0.3	50%	0.02
<i>Polygonella articulata</i> (L.) Meisn.	40%	<0.1	13%		27%	<0.1	100%	0.1		
<i>Juniperus virginiana</i> L.	60%	0.7							100%	1.9
<i>Dichanthelium depauperatum</i> (Muhl.) Gld	60%	0.5	25%	<0.1	9%				50%	<0.1

Table 5 continued

	Beach Heather Dune Shrubland		Sandplain Heathland (A. uva-ursi and C. conradii co-dominant)		Sandplain Heathland (A. uva- ursi dominant)		Dune Swale Heath		Orchard Grass Pasture/Sandplain Grassland	
	fr.	X	fr.	X	fr.	X	fr.	X	fr.	X
<i>Dichanthelium acuminatum</i> (Sw.) Gld	40%	<0.1	25%	<0.1	18%	0			50%	<0.1
<i>Rumex</i> spp. L.	20%	<0.1	13%	0.1					100%	0.4
<i>Prunus maritima</i> Marsh.	20%		13%		45%	0.2			50%	2.2
<i>Hudsonia tomentosa</i> Nutt.	80%	7.84	38%	1.9	9%	0.3				
<i>Achillia millefolium</i> L.					18%	<0.1			100%	<0.1
<i>Solidago odora</i> Ait.	20%				45%	<0.1			50%	<0.1
<i>Solidago bicolor</i> L.			13%						100%	<0.1
<i>Trifolium arvense</i> L.			13%	<0.1					100%	<0.1
<i>Juncus greenii</i> Oakes & Tuckerman					9%	<0.1			100%	<0.1
<i>Comptonia peregrina</i> (L.) Coult			50%	0.1	55%	2.0				
<i>Lechea mucronata</i> Raf	40%	<0.1							50%	0.9
<i>Helianthemum canadense</i> (L.) Michx.			13%		27%	<0.1			50%	<0.1
<i>Melampyrum lineare</i> Desr.	20%	<0.1			18%	<0.1			50%	<0.1
<i>Rubus</i> spp. L.	20%	<0.1			18%				50%	<0.1
<i>Hieracium gronovii</i> L.					36%	0.6			50%	<0.1
<i>Gaylussacia baccata</i> (Wangenh.) Kch	20%	0.1	38%	0.1	27%	0.7				
<i>Quercus alba</i> L.	40%	<0.1	25%	0.1	18%	1.2				
<i>Rosa carolina</i> L.			13%		18%	0.1			50%	<0.1
<i>Solidago puberula</i> Nutt.					27%	<0.1			50%	<0.1
<i>Prunus serotina</i> Ehrh.	40%	0.8	25%	0.4	9%					
<i>Maianthemum stellatum</i>					18%	0.6			50%	<0.1
<i>Asclepias</i> spp. L.			13%						50%	<0.1
<i>Panicum</i> spp. L.			13%	0.5			50%	<0.1		
<i>Quercus velutina</i> Lam.	40%	0.4	13%	0.1	9%	0.1				
<i>Dichanthelium linearifolium</i> Gld	20%	0	13%		9%					
<i>Toxicodendron radicans</i> (L.) Kuntze	20%	0.2	13%	0.1						
<i>Vaccinium pallidum</i> Ait.			13%	0.1	18%	<0.1				

Table 6. Significant results from tests of physical features and land use categories between vegetation groups determined by cluster analysis.

	<i>Northern Beach Heather Dune Shrubland</i>	<i>Sandplain Heathland (A. uva- ursi and C. conradii co- dominant)</i>	<i>Sandplain Heathland (A. uva-ursi dominant)</i>	<i>Dune Swale Heath</i>	<i>Sandplain Grassland</i>		
<i>Physical Feature Categories</i>	(n=5)	(n=8)	(n=11)	(n=2)	(n=2)	<i>G</i>	<i>P</i>
Soil Type	HoC	CdA-C	HoC/CdB	HoC	CdD	25.20	0.194
Surface Geology	P/O	Pa	Oa	P	O/D	20.24*	0.009
<i>Land use categories</i>						<i>G</i>	<i>P</i>
Cover 1848	R	R ^a	R	D ^a	R/C	21.45*	0.044
Cover 1949	S/B	B ^a	B	D ^a	R/B	26.54*	0.047
Impact Index	S/H ^a	H ^b	S	D ^{ab}	H	17.47*	0.026

G tests for independence were conducted on physical feature categories. Significant results are indicated by an asterisk ($\alpha=0.05$); post hoc comparisons were conducted on significant results.

Physical Feature Categories: Typical soil type and geology of the cluster (Fletcher 1993).

-Soil Type: CdA-D = Carver Course Sand w/slopes 0-35%; HoC = Hooksan Sand

-Surface Geology: P = Post Glacial; O = Glacial Outwash; D = Developed.

Land use categories indicated are typical for the cluster.

-Vegetation types: R = rough pasture (open landscape used to pasture livestock); B = brush and rough pasture (open landscape with some brush and stunted trees, used to pasture livestock); D = dune areas with active eolian processes, found mostly in Provincetown; S = sandy waste (open area with little or no vegetation); C = cultivated area

-*Impact index:* This index was generated from interpretation of historical maps and photographs: D = dune field (active eolian processes); S = secondary succession vegetation (area that may have been cleared for pasture, wood lot etc. but any activity had ceased for the last 100 yrs); H = high impact area (areas that were highly disturbed within the last 50 years; e.g., sand pit, powerline right-of-way, former military base)

Figure 1a-b. Open areas of CCNS, 1949 and 2000. Black areas represent open areas of CCNS. Boxes indicate largest areas of contiguous open habitat in 2001.

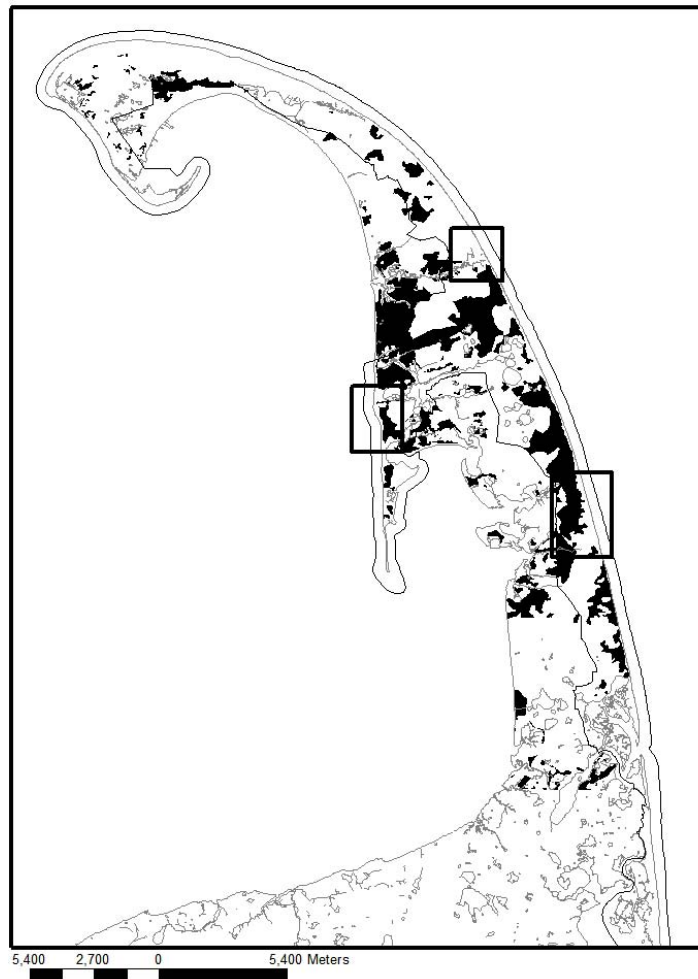


Figure 1a. Open area of Lower Cape Cod 1949

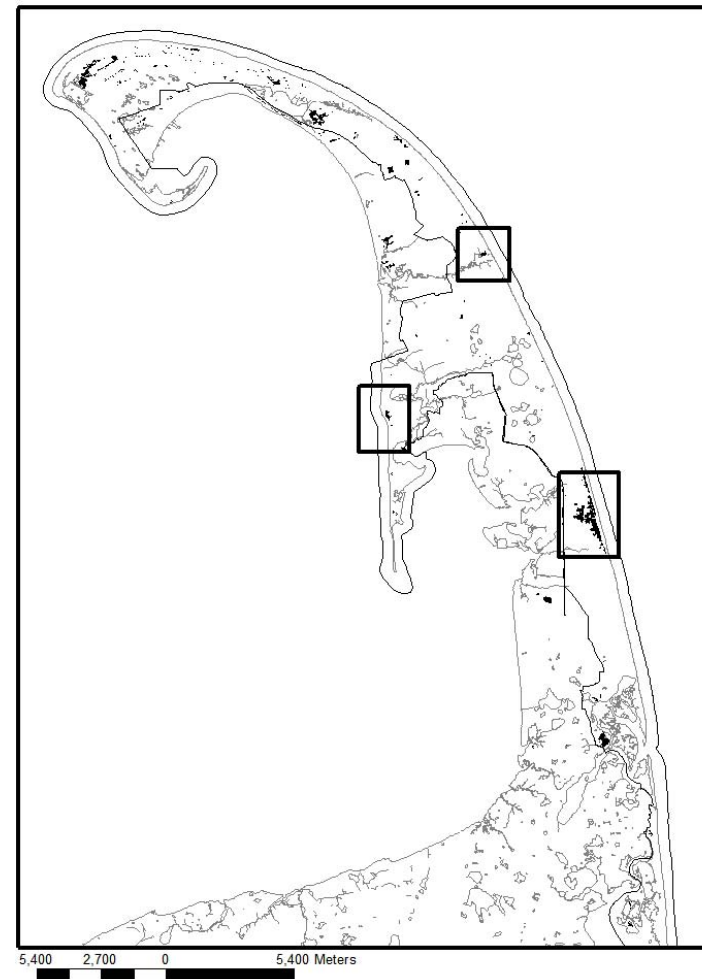


Figure 1b. Open areas of Lower Cape Cod 2000

Figure 2. Location of CCNS coastal sandplain heathland sample sites. Circles indicate sites surveyed in 1988, 1999, and 2003. Diamonds indicate sites sampled only in 2003. The black line indicates the Park boundary. (Not pictured: barrier beach system in Chatham within CCNS boundary. No monitoring sites or extensive sandplain plant communities present in this area)



Figure 3. Locations of three sites for studying successional processes in coastal heathlands at CCNS.

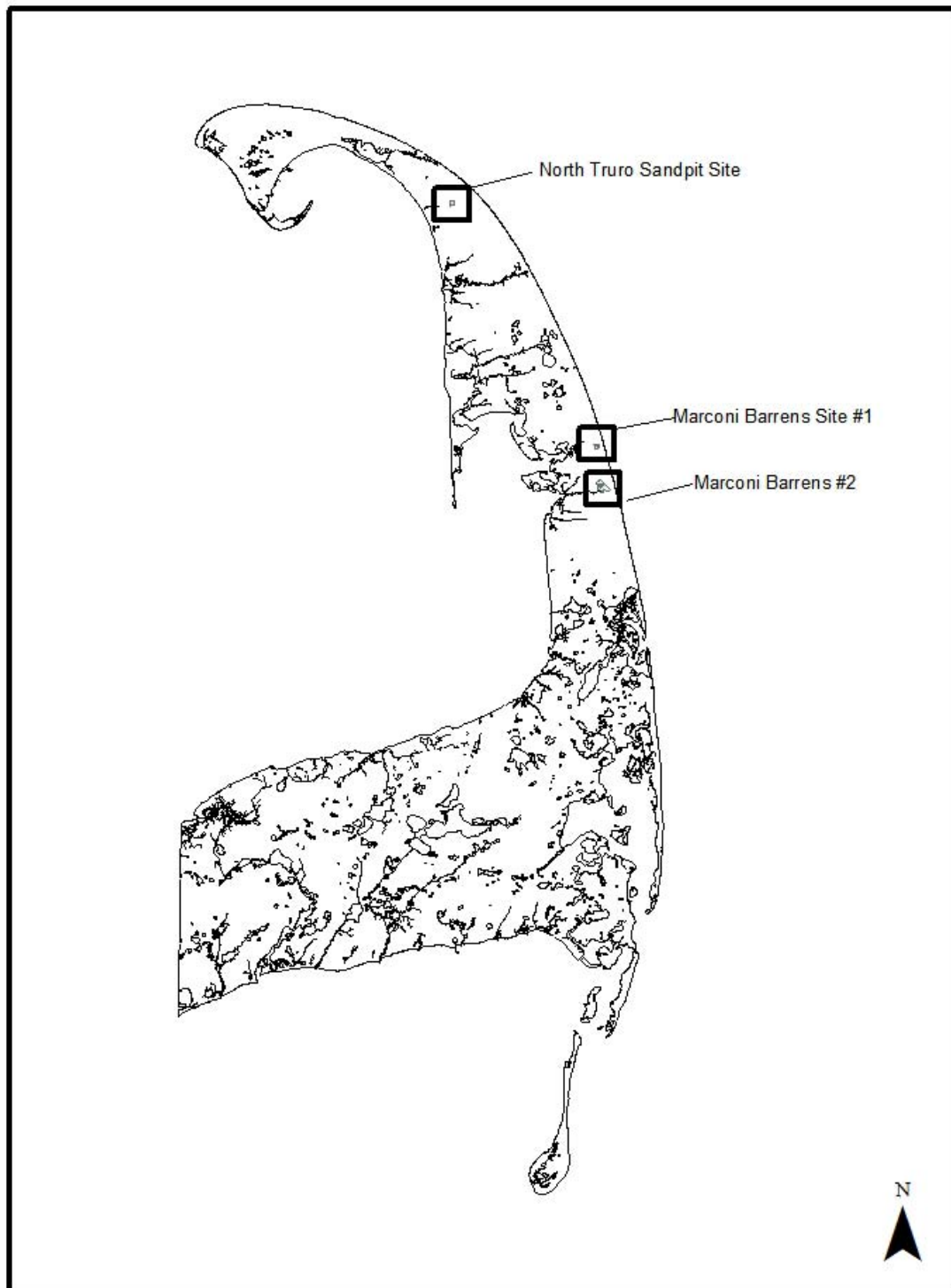


Figure 4. Diagram of permanent plots established by Carlson et al. (1992) and resurveyed in 1999. Plots are 20 m x 10 m and contain three transects composed of ten 0.25-m by 1-m subplots. Vegetation cover was estimated (with cover classes) for all vascular and non-vascular species encountered.

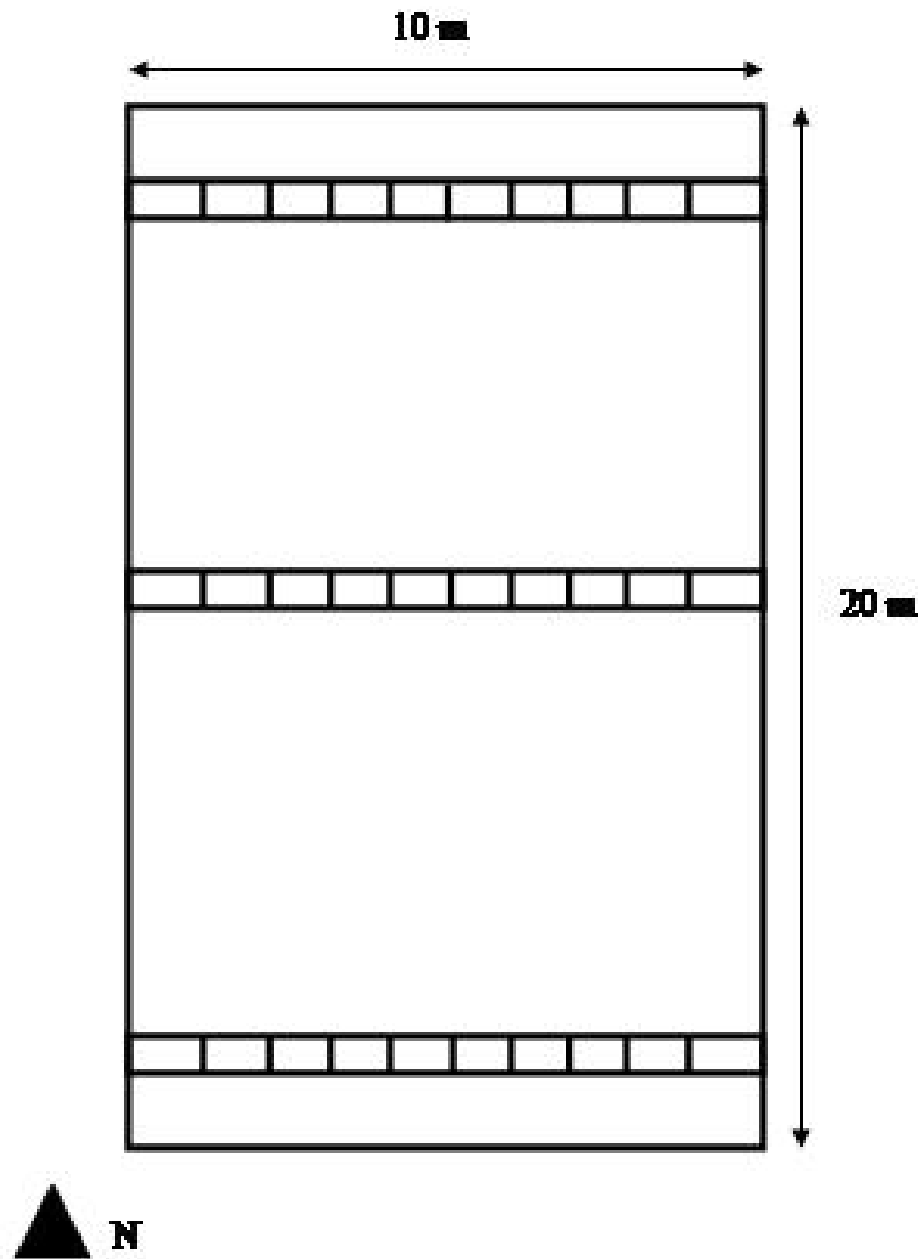
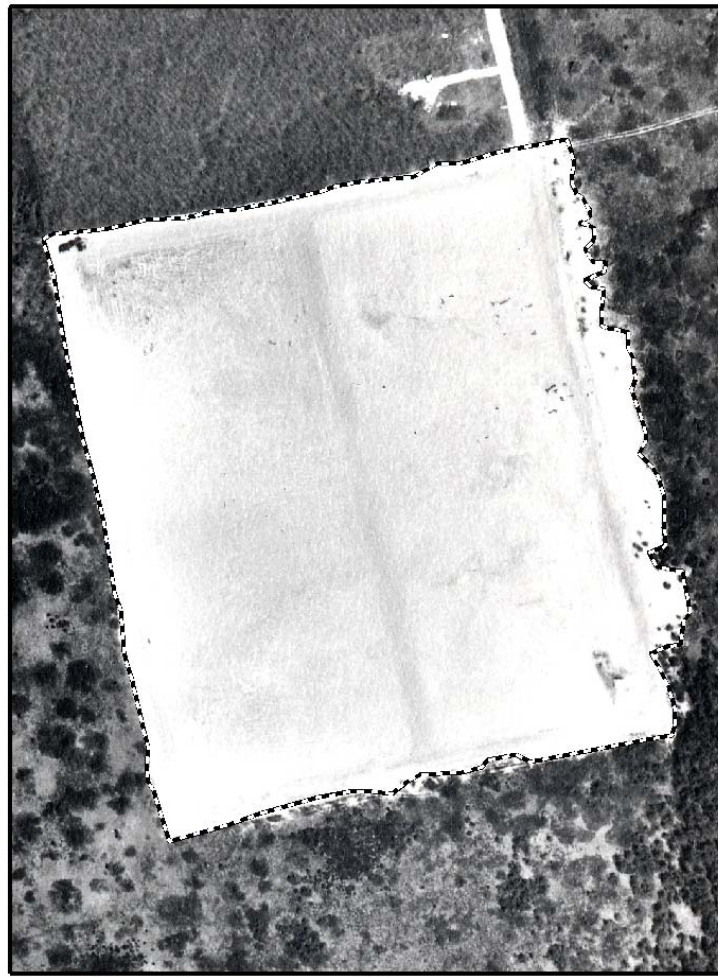
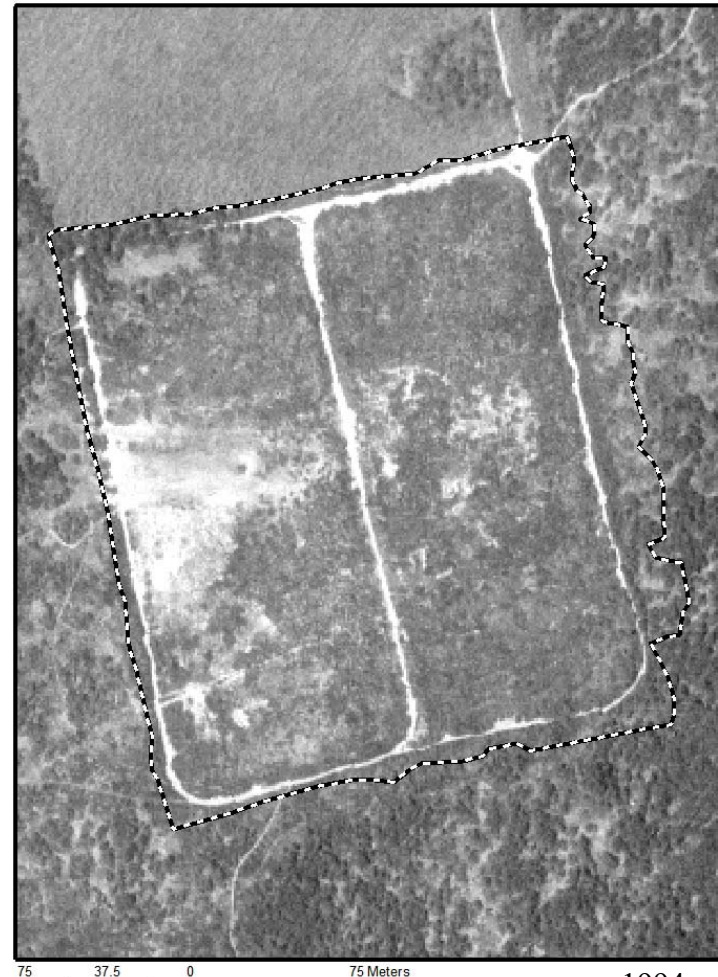


Figure 5a. Images of North Truro Sandpit site from 1960 (1:7200) and 1994 (1:5000) aerial photographs. The white area is bare sand. Most of the topsoil (~1m) was removed in 1958 for a sandpit and subdivision.



1960



1994

Figure 5b. Images of the Marconi Barrens Site #1 from 1960 (1:7200) and 1994 (1:5000) aerial photographs. The Marconi Barrens Sites were located at the former Camp Wellfleet, an Army training facility actively used from 1943 to 1961. Site #1 was used as a storage area for munitions during and after World War II (U.S. Corps of Engineers 1994). The study site is identified with hatched outline. The area was scraped to mineral earth with a bulldozer removing all vegetation.

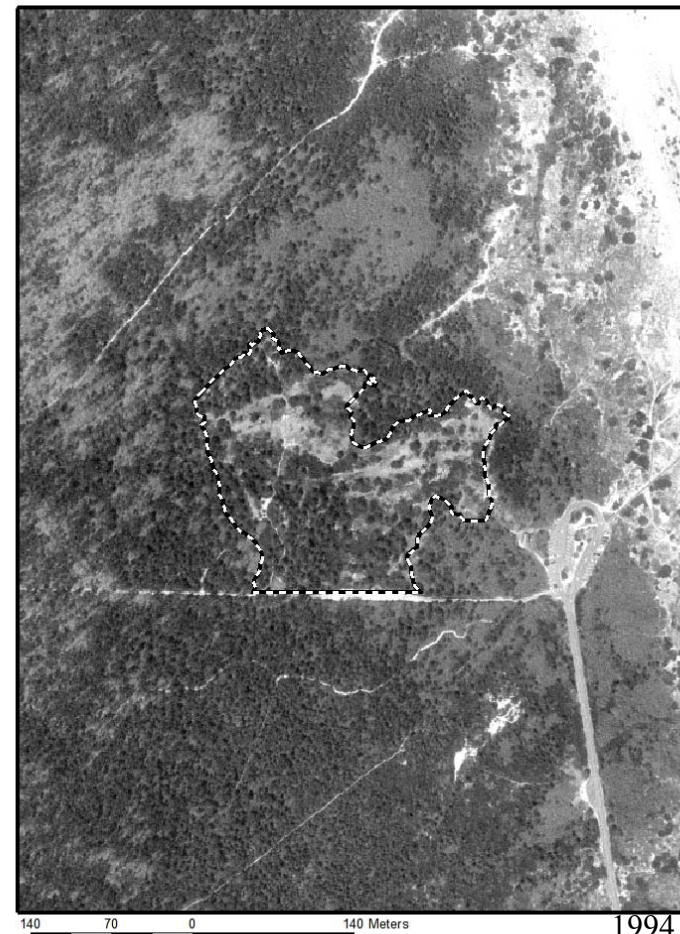
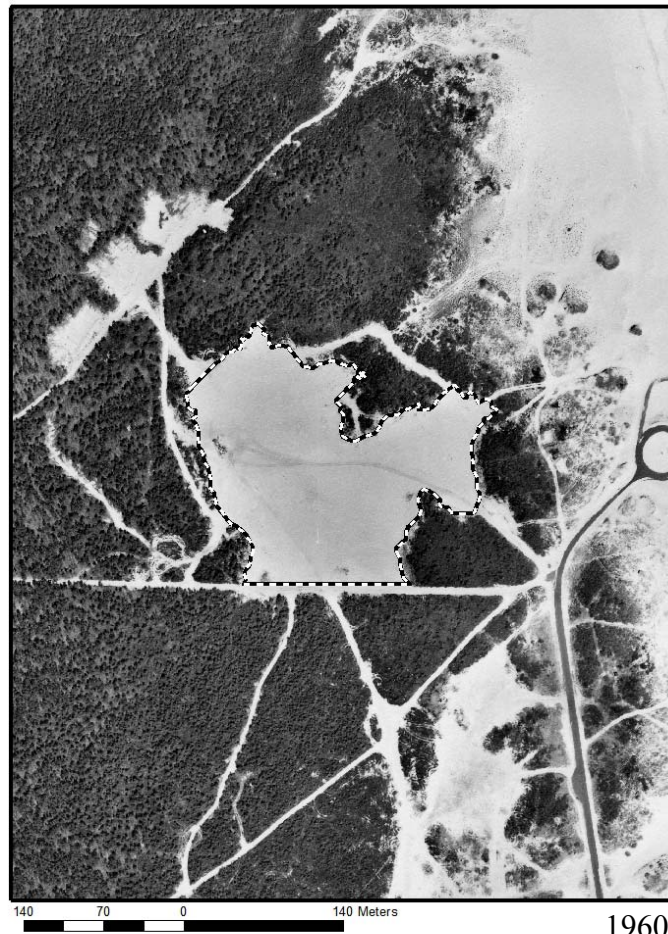


Figure 5c. Images of the Marconi Barrens Site #2 from 1947 (1:1500) and 1994 (1:5000) aerial photographs. This site was used as bombing range (up to 1000-lb bombs) and as a storage area for munitions (US Corps of Engineers 1994). It also was graded repeatedly with a bulldozer. Vegetation was removed from the sample area in the early 1940's (delineated by the hatched line).

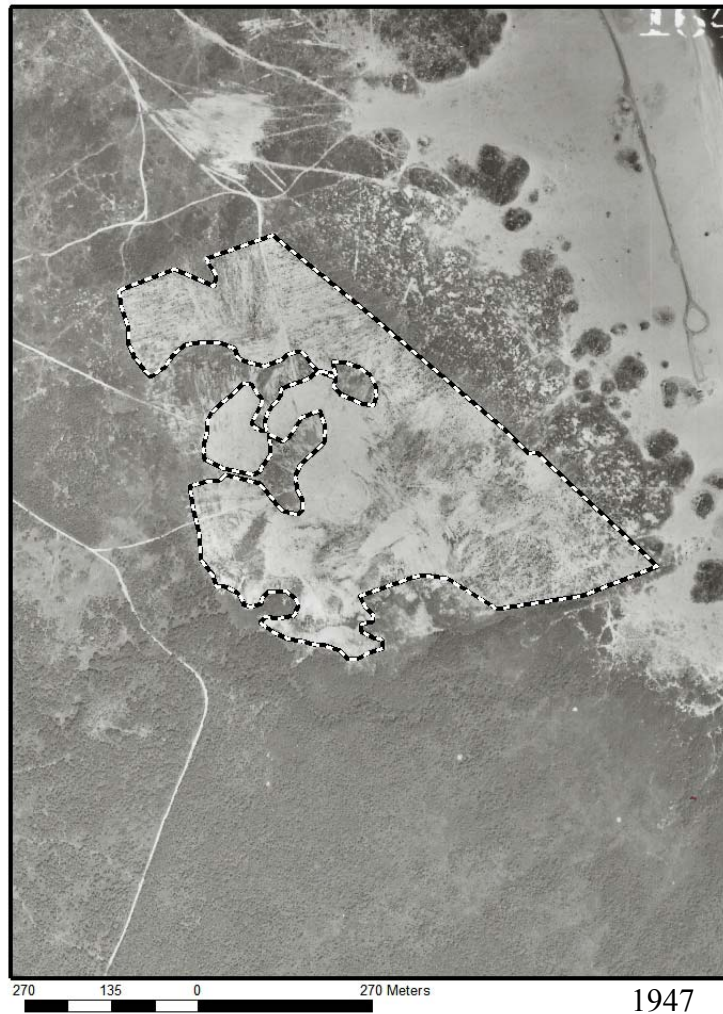
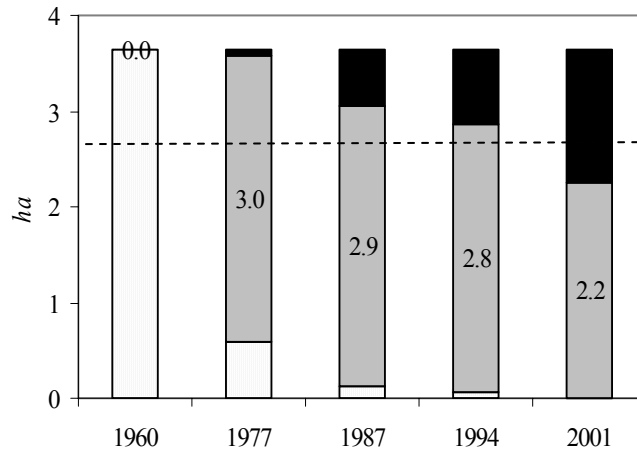
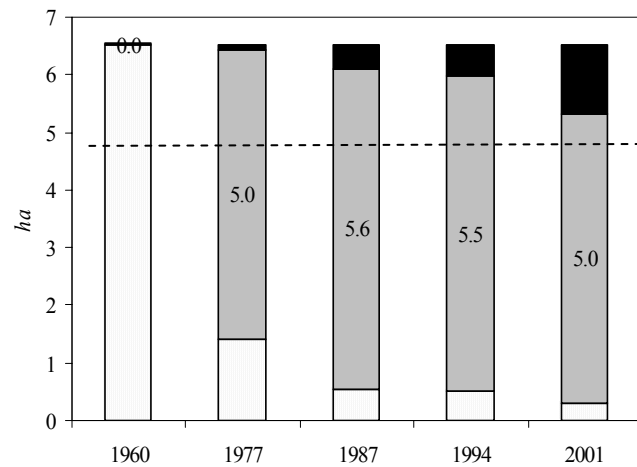


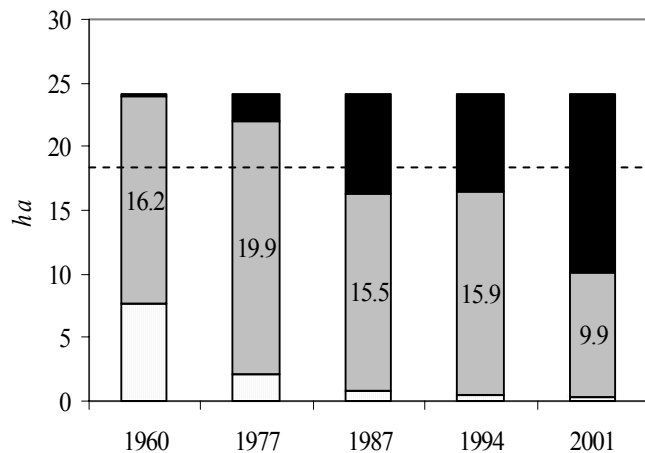
Figure 6 a-c. Change in vegetation at three sample sites 1960-2001. All activity at the sites had ceased by 1961. The 1960 photo set was chosen to use as the start point for analysis. Hatched indicates area of bare sand, grey ground cover < 1-m, black, ground cover > 1-m. Numbers in bars are area of ground cover <1-m (ha).



a. North Truro Site

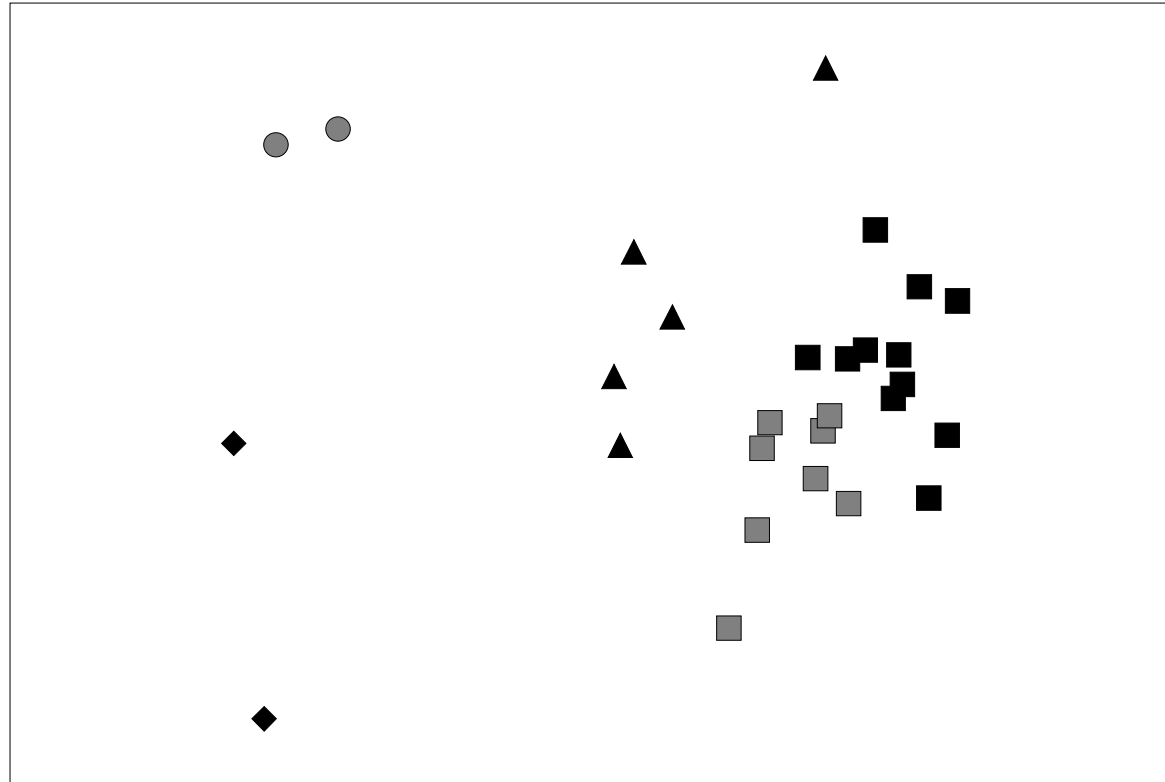


b. Marconi Barrens Site #1



c. Marconi Barrens Site #2

Figure 7. Two-dimensional MDS ordination of coastal sandplain heathland and grassland sample sites based on species cover data.



Northern beach heather dune shrubland ▲ Sandplain heathland (*A. uva-ursi* and *C. conradii* co-dominant) ■ Sandplain heathland (*A. uva-ursi* dominant) ■ Dune swale heathland/grassland ◇ Sandplain grassland ○

Figure 8a. Photograph of beach heather heathland



Figure 8b. Photograph of Sandplain Heathland (*A. uva-ursi* and *C. conradii* co-dominant)



Figure 8c. Photograph of *A. uva-ursi* dominant



Figure 8d. Photograph of dune swale heathland



Figure 8e. Photograph of sandplain grassland



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APPENDIX A

Appendix A contains results from various analyses on species environmental and land use characteristics. The results were not significant for the most part; those data indicated significant differences between the groups delineated by cluster analysis were from a data set containing species characteristic information. This data set did not contain information about all of the species encountered in the study. It has thus been placed in the appendix and results should be considered strictly exploratory and speculative, however, it may serve as a launch pad for investigations between certain ecological functions of species assemblages.

The results of the analysis indicates that the impact (i.e., greater abundance) of native species (primarily Ericaceae) is greater in both of the sandplain heathland groups than in the beach heather group, with the rare sub-shrub *C. conradii* differentiated the sandplain heathland (*A. uva-ursi* and *C. conradii* co-dominants) from the other heathland groups. Non-native and invasive species have a greater impact in the beach heather (primarily *A. millefolium*) and especially the number and impact of invasive and non-native grasses in the sandplain grassland group. The sandplain grassland group is separated from the sandplain heathland groups by the impact of grasses, especially Juncaceae.

Median value of species characteristic and impact indices by vegetation groups identified by cluster analysis. Data used to compile table from the PLANTS Database (USDA NRCS 2004).

Species characteristics are the median value for the cluster. Values are estimated on a continual scale from zero (low) to ten (high). Data used to compile species characteristics from the PLANTS Database (USDA NRCS 2004). Not all species encountered were used to generate species characteristic median index values (see Appendix B for species list).

- Adapted to fine/course textured soils: Plant capability to establish and grow in fine or coarse textured soils
- pH, (max/min/mean): pH under which this plant can maintain good growth
- C:N ratio: Carbon:nitrogen ratio of the plant material
- Salinity Tolerance: Plant's tolerance to saline soil conditions
- Shade Tolerance: Relative tolerance for this plant to grow in shade conditions.
- Fire Tolerance: Relative tolerance to fire, i.e., can it re-sprout, re-grow, or re-establish from seed after a fire?
- Bloom Period: Seasonal period in the U.S. that the plants bloom the most
- Active Growth Period: Plants: Seasonal period with most active growth

Species Characteristic Impact Indices: Median “impact index” values for each group are displayed (impact index is the sum of the cover value for all species with the particular species characteristic for each site), followed by the median number of species with that characteristic in parenthesis. Not all species encountered were used to generate species characteristic median index values (see Appendix B for species list).

	Northern Beach Heather Dune Shrubland	Sandplain Heathland (<i>A. uva-ursi</i> and <i>C. conradii</i> co-dominant)	Sandplain Heathland (<i>A. uva- ursi</i> dominant)	Dune Swale Heath	Sandplain Grassland		
<i>Species Characteristics</i>	(n=5)	(n=8)	(n=11)	(n=2)	(n=2)	H	P
<i>pH (Minimum)</i>	4.9	5.0	5.2	5.1	5.1	1.40	0.845
<i>pH (Maximum)</i>	7.3	7.4	7.6	7.5	7.2	4.45	0.349
<i>pH (MEAN)</i>	6.1	6.2	6.4	6.3	6.1	2.94	0.569
<i>C:N Ratio</i>	8.0	7.9	7.5	6.3	7.0	3.77	0.438
Low (0) <--Mid (5)-->High (10)							
<i>Salinity Tolerance</i>	4.3	2.4	1.5	3.8	2.2	4.12	0.390
<i>Shade Tolerance</i>	4.5	3.6	4.0	6.0	3.8	7.69	0.104
<i>CaCO3 Tolerance</i>	6.0	5.0	5.3	5.3	5.0	4.31	0.365
<i>Fire Tolerance</i>	4.4	5.3	5.3	7.5	5.1	6.17	0.186
Early Spring (1)<-->Fall(8)							
<i>Bloom Period</i>	5.0	4.3	4.8	4.4	4.7	4.37	0.358
<i>Active Growth Period</i>	5.3	5.3	5.5	4.6	4.9	9.26	0.055
<i>Species Characteristic Impact Indices</i>							
<i>Native Species</i>	47.1 ^{ab} (16)	96.0 ^a (13)	111.3 ^b (15)	32.3 (9)	59.6 (27.5)	16.29*	0.002
<i>Non-native Species</i>	0.0	0.0	0.0	0.0	1.6 (8.5)	10.87*	0.028
<i>Invasive Species</i>	0.4 ^a (1)	0.0	0 ^a	0.0	3.1 (9)	13.96*	0.007
<i>Rare Species</i>	0	29.0 (1)	6.0 (1)	0.0	0.1 (0.5)	16.85*	0.002
<i>Asteraceae</i>	0.1 (3)	<0.1 (1)	0.1 (2)	0.1 (0.5)	0.9 (8)	7.55	0.109
<i>Fagaceae</i>	0.3 (1)	0.8 (1)	2.6 (1)	0.0	0.6 (1)	7.43	0.115
<i>Pinaceae</i>	7 (1)	19.6 (1)	9 (1)	5.9 (1)	3.8 (1)	3.21	0.523
<i>Ericaceae</i>	13.5 ^a (1)	36.1 ^b (2.5)	70.0 ^{ab} (2)	19.0 (2)	3.6 (1.5)	19.24*	>0.000
<i>Cyperaceae</i>	0.4 (1)	0.5 (1)	0.1 (1)	0.1 (0.5)	1.1 (1)	7.39	0.117
<i>Juncaceae</i>	0.0	0 ^a	0 ^b	0.4 (0.5)	<0.0 ^{ab} (1)	21.96*	>0.000
<i>Poaceae</i>	0.7 (4)	0.4 (3)	1.6 (2)	6.3 (2)	43.2 (5)	3.26	0.515

Median environmental factor values by group identified by cluster analysis. Soil from each sample site were collected and analyzed. None of the tests (Kruskal-Wallis) detected significant differences between groups.

<i>Environmental Factors</i>	<i>Northern Beach Heather Dune Shrubland</i> (n=5)	<i>Sandplain Heathland (A. uva- ursi and C. conradii co-dominant)</i> (n=8)	<i>Sandplain Heathland (A. uva-ursi dominant)</i> (n=11)	<i>Dune Swale Heath</i> (n=2)	<i>Sandplain Grassland</i> (n=2)	H	P
<i>Clay + Silt (%)</i>	2.52	4.62	2.53	2.40	9.50	4.22	0.377
<i>TEC</i>	1.36	1.93	2.45	0.76	4.22	6.22	0.184
<i>pH</i>	5.62	5.07	5.33	5.71	4.80	2.10	0.718
<i>%C*</i>	0.38	0.82	0.73	0	n.d.	5.04	0.280
<i>OM (%)</i>	0.74	1.09	0.74	0.43	1.40	4.47	0.346
<i>Ca (mg/kg)</i>	157.75	127.67	154.50	87.42	90.00	6.49	0.165
<i>Mg (mg/kg)</i>	36.83	27.00	31.00	26.17	24.00	4.16	0.385
<i>Fe (mg/kg)</i>	107.08	141.25	137.33	46.42	157.00	5.81	0.213
<i>Al (mg/kg)</i>	541.67	568.75	508.67	61.17	832.00	5.61	0.230
<i>Dist. to Ocean (m)</i>	219.00	802.50	324.00	988.00	748.50	5.78	0.216

* data from only four groups used for this test

Environmental Factors: Median value for the group.

-Clay and silt: Median value of percent clay and silt for each cluster group.

-TEC: Median total exchange capacity (m.e./100 g soil) by cluster group

-pH: Median value of soil pH for each cluster group.

-%C: Median value of percent carbon from analysis of soil samples by cluster group.

-OM: Median percent value of organic material in soil sample.

-Ca and Mg: Median value (mg/kg) of anion in soil sample from sites in each cluster group.

-Dist to Ocean: Median distance (m) from approximate center of sample sites to either the Atlantic Ocean or Cape Cod Bay in each group.

Appendix B. List of species used for characteristic and impact indices analysis
(Appendix A). Data from U.S.D.A. N.R.C.S. (2004).

<i>Achillea millefolium</i> L.	<i>Quercus velutina</i> Lam.
<i>Acer rubrum</i> L.	<i>Rosa carolina</i> L.
<i>Ammophila breviligulata</i> Fern.	<i>Rosa rugosa</i> Thunb.
<i>Aralia nudicaulis</i> L.	<i>Rosa virginiana</i> P. Mill.
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	<i>Rubus allegheniensis</i> Porter
<i>Asclepias tuberosa</i> L.	<i>Rubus flagellaris</i> Willd.
<i>Baptisia tinctoria</i> (L.) R. Br. ex Ait. f.	<i>Rubus hispidus</i> L.
<i>Bromus inermis</i> Leyss.	<i>Sassafras albidum</i> (Nutt.) Nees
<i>Carex scoparia</i> Schkuhr ex Willd.	<i>Saponaria officinalis</i> L.
<i>Chimaphila umbellata</i> (L.) W. Bart.	<i>Salicornia virginica</i> L.
<i>Corylus americana</i> Walt.	<i>Scirpus cyperinus</i> (L.) Kunth
<i>Comptonia peregrina</i> (L.) Coult.	<i>Schizachyrium scoparium</i> (Michx.) Nash
<i>Dactylis glomerata</i> L.	<i>Smilax glauca</i> Walt.
<i>Deschampsia flexuosa</i> (L.) Trin.	<i>Smilax rotundifolia</i> L.
<i>Elymus repens</i> (L.) Gould	<i>Solidago gigantea</i> Ait.
<i>Erigeron philadelphicus</i> L.	<i>Solidago nemoralis</i> Ait.
<i>Erigeron strigosus</i> Muhl. ex Willd.	<i>Solidago rugosa</i> P. Mill.
<i>Leucanthemum vulgare</i> Lam.	<i>Solidago sempervirens</i> L.
<i>Photinia pyrifolia</i> (Lam.) Robertson & Phipps	<i>Symphyotrichum novi-belgii</i> (L.) Nesom var. <i>novi-belgii</i>
<i>Populus grandidentata</i> Michx.	<i>Symphyotrichum patens</i> (Ait.) Nesom var. <i>patens</i>
<i>Poa pratensis</i> L.	<i>Typha latifolia</i> L.
<i>Prunus americana</i> Marsh.	<i>Vaccinium angustifolium</i> Ait.
<i>Prunus maritima</i> Marsh.	<i>Vaccinium corymbosum</i> L.
<i>Prunus serotina</i> Ehrh.	<i>Vitis aestivalis</i> Michx.
<i>Pteridium aquilinum</i> (L.) Kuhn	<i>Vicia cracca</i> L.
<i>Quercus alba</i> L.	

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